

Is *Ovophis okinavensis* Active Only in the Cool Season? Temporal Foraging Pattern of a Subtropical Pit Viper in Okinawa, Japan

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Yohei Kadota (2011) Is *Ovophis okinavensis* active only in the cool season? Temporal foraging pattern of a subtropical pit viper in Okinawa, Japan. *Zoological Studies* 50(3): 269-275. Snakes are usually active in the warm season rather than the cool season because they are ectothermic animals that rely on external heat sources to maintain their body temperatures. However, previous studies on *Ovophis okinavensis* showed that this snake is most active in winter to early spring, presumably to exploit actively breeding frogs. This unusual activity pattern of *O. okinavensis* may simply reflect the fact that the availability of prey animals is restricted to this season, which obliges the snake to engage in feeding activities during periods of low temperatures. To test this hypothesis, I examined seasonal activity patterns of both *O. okinavensis* and frogs in the study area, where several species of frogs aggregate for breeding from winter to summer. Emergence sites of snakes well corresponded to those of frogs. Snakes and frogs were frequently found in both the warm and cold seasons. The daily emergence number of snakes was strongly correlated with that of frogs. These results suggest that *O. okinavensis* exhibits a foraging strategy that is adjusted to spatial and temporal fluctuations of the emergence of frogs. <http://zoolstud.sinica.edu.tw/Journals/50.3/269.pdf>

Key words: Seasonal activity, Snake, Viperinae, Ryukyu Archipelago, Frogs.

To feed efficiently, many animals adjust their activities to seasonal changes in climate and prey availability in their native habitats (Hirai 2004, Prange et al. 2004, Santos et al. 2007), because both abiotic and biotic factors may affect an individual's growth, reproduction, and survival, which ultimately influence population viability. Understanding how animals respond to changes in climate and food availability is an important goal in ecology. In temperate and subtropical regions, the activities of snakes generally decline with decreasing temperature (Gibbons and Semlitsch 1987, López and Giraudo 2008), because snakes are ectotherms that rely on external heat sources to maintain their body temperature so that they can carry out their physiological and behavioral activities (Huey 1982, Lillywhite 1987).

Ovophis okinavensis is a short, stout-bodied viperid snake that inhabits forested areas,

especially near streams, ponds, and marshes, on subtropical islands of the Okinawa and Amami groups, Ryukyu Archipelago, Japan (Takara 1962). This snake is primarily terrestrial and nocturnal (Koba 1962, Moriguchi 1989) and is considered a typical ambush predator (Takara 1962). Its diet consists of frogs, lizards, snakes, birds, and small mammals (Mori and Moriguchi 1988, Kadota 2006). Although *O. okinavensis* exhibits such broad food habits as a species, diets of some local populations almost exclusively consist of frogs (Ikehara and Akamine 1976, Moriguchi 1989, Mori et al. 2002).

Previous ecological studies on *O. okinavensis* in the northern mountains of Okinawa I. (Ikehara and Akamine 1976, Moriguchi 1989, Mori et al. 2002) showed that this snake is most active in winter to early spring (Dec.-Mar.). Those authors suggested that the activity pattern of the snake is highly associated with the breeding activities of

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frogs that aggregate for breeding in winter (*Rana narina* and *Rana* sp., formerly *R. okinavana*; see Matsui 2007, for the current taxonomic status of this species) or from winter to early spring (*Rhacophorus viridis*). The highest activity of *O. okinavensis* occurring in the low-temperature period of the year is inconsistent with the general activity pattern of snakes in temperate and subtropical regions, suggesting that this is an exceptional case of low-temperature preference among snakes (Mori et al. 2002). However, it is possible that the high activity in the low-temperature period simply reflects the fact that the availability of prey animals is restricted to this season, which obliges the snake to engage in feeding activities at low temperatures. If this were true, it would be expected that *O. okinavensis* would emerge even during the warm season at sites where prey animals are abundant throughout the year.

To test this expectation, I carried out a field study on the feeding habits of *O. okinavensis* and examined seasonal activity patterns of both *O. okinavensis* and frogs in the northern mountains of Okinawa I., where several species of frogs aggregate for breeding from winter to summer (Dec.-Aug.). I then analyzed the effects of frog activities and climate conditions on the foraging activity patterns of the snake.

MATERIALS AND METHODS

Field surveys were carried out along a selected section of a forest road (which was 2.2 km long and 5 m wide) in the northern part of Okinawa I., Ryukyu Archipelago, Japan (26°46'N, 128°14'E). The study area is located 6 km northwest and 4.5 km southwest of the field sites of Ikehara and Akamine (1976) and Mori et al. (2002), respectively. The road is surrounded by grassy slopes and a *Castanopsis sieboldii* forest. A gutter runs along 1 side of the road and has a total of 26 water-gathering structures (WGSs) at irregular intervals. Most of the WGSs are square cavities (approximately 1 m³) without a cover, and contain 10-40 cm of stagnant water throughout the year. These WGSs are used as oviposition sites by frogs (see "RESULTS"). Other permanent water bodies available in the study area include several streams that run across or under the road.

I carried out a route census by slowly walking on the road with the aid of a flashlight to search for *O. okinavensis* and frogs at night.

When snakes and frogs were found within 3 m of a WGS, I classified them as being located in the WGS area. All other areas were defined as non-WGS areas. Each time I encountered a snake, I recorded the date, time, and location, and caught it with a snake hook. The snout-vent length (SVL) and body mass (BM) of captured snakes were measured, and snakes were sexed using a sexing probe, by manual eversion of the hemipenis, and/or examination of the external shape of the tail base. Stomach contents were examined by forced regurgitation. Prey items were identified to the lowest possible taxonomic level, fixed in 10% formalin, and later preserved in 70% ethanol. Each snake was marked by inserting a small passive integrated transponder (PIT) tag under the skin for permanent identification and by painting a unique number on the dorsal surface of the head and posterior part of the body for short-term identification. The snakes were released at the site of capture as quickly as was possible. To minimize disturbance, I did not capture marked snakes if their preceding capture had occurred within 1 mo. I only recorded the time and location of those snakes. Between July 2002 and Nov. 2004, 69 night surveys were conducted.

When a frog was found during the census, I identified it to species level. In each WGS and non-WGS section between adjacent WGSs, the number of frogs of each species was counted, and an estimate was also made from the number of mating calls. For the subsequent analysis, I used the larger of these numbers as the number of frogs in each WGS and each intervening section. Data for frogs were obtained in Mar. 2003 - Nov. 2004. Data of daily precipitation and humidity were obtained from the Japan Weather Association, Okinawa Branch at Nago City (~40 km southwest of the study site). Daily air temperature was measured at the beginning of each survey.

To compare the frequency of WGS use by snakes and frogs with the availability of WGSs in the survey area (the proportion of total WGS areas to the total surface area of the road), I used a Chi-squared test. To examine relationships between the numbers of snakes and frogs observed in each WGS area, I used Spearman's rank correlation coefficient. The level of statistical significance for these analyses was set to 0.05. I used generalized linear models (GLMs; Crawley 2002) in the software R 2.1 to examine the effects of each frog species (6 species, see "RESULTS") and 3 climatic factors (precipitation, humidity, and air temperature) on the daily emergence of snakes.

In the models, I fit the number of each frog species and each climate factor as explanatory terms against the total daily number of snakes as a response term. I used the restricted maximum-likelihood model (REML) to decompose the variances and derive parameter estimates using Poisson errors and a log-link function. Based on the Akaike information criterion (AIC; Burnham and Anderson 2002), the 5 best-fitting models were selected and evaluated.

RESULTS

In total, 297 records (229 males, 64 females, and 4 unsexed snakes) were obtained for 97 (75 males and 22 females) individuals of *O. okinavensis*. The mean (\pm S.E.) SVL was 429 ± 5.6 (range, 295-511) mm and BM was 85 ± 4.2 (range, 24-219) g for males and 526 ± 21.7 (range, 214-621) mm and 195 ± 16.3 (range, 39-310) g for females, respectively. The WGSs were used for oviposition sites by 5 species of frogs. The main reproductive seasons of the frogs were as follows: *Rana* sp. (Rs) during a short period in Dec., *Rhacophorus viridis* (RV) from Jan. to May, *Microhyla okinavensis* (MO) from Mar. to Aug., *Buergeria japonica* (BJ) from Apr. to Sept., and *Polypedates leucomystax* (PL) from June to Sept. Although *Rana narina* (RN) did not use the WGSs for reproduction, it was abundant at the study site.

In total, 49 prey items were obtained from 29 snakes. Among them, 89.8% were frogs (44 of 49), of which *M. okinavensis*, *Rana* sp., *Rha. viridis*, *P. leucomystax*, and *R. narina* comprised 38.6%,

29.6%, 20.5%, 9.1%, and 2.3%, respectively. The remaining food items were 2 shrews (*Crociodura watasei*) and 3 lizards (*Ateuchosaurus pellopleurus*, *Goniurosaurus kuroiwaie kuroiwaie*, and *Takydromus smaragdinus*). *Microhyla okinavensis*, *Rana* sp., and *Rha. viridis* were mainly found in stomach contents in Mar.-June, Dec.-Jan., and Jan.-Mar., respectively (Table 1).

Although WGS areas occupied only 2% of the total area of the study site, 81.2% of snakes and 75.3% of 5 species of frogs (all but *R. narina*) were found within WGS areas. On the other hand, almost all *R. narina* (98.7%) were found outside of WGS areas. Snakes and the 5 species of frogs were found in WGS areas more frequently than expected from a random distribution (Chi-squared test, snake, $d.f. = 1$, $\chi^2 = 1716.7$, $p < 0.001$; PL, $d.f. = 1$, $\chi^2 = 458.05$, $p < 0.001$; MO, $d.f. = 1$, $\chi^2 = 931.9$, $p < 0.001$; BJ, $d.f. = 1$, $\chi^2 = 824.51$, $p < 0.001$; RV, $d.f. = 1$, $\chi^2 = 856.79$, $p < 0.001$; Rs, $d.f. = 1$, $\chi^2 = 724.61$, $p < 0.001$; RN, $d.f. = 1$, $\chi^2 = 0.762$, $p = 0.383$; Fig. 1). There were significant positive correlations between the total number of snakes and that of *Rha. viridis*, and between the total number of snakes and that of *M. okinavensis* in each WGS area (Spearman's rank correlation coefficient, RV, $r = 0.528$, $p = 0.029$; MO, $r = 0.447$, $p = 0.025$; Fig. 2). No significant relationships were detected between the number of snakes and that of the other frogs in each WGS area (Fig. 2).

Snakes and frogs were frequently found in the warm season (Mar.-June) as well as in the cold season (Dec.-Feb.) (Fig. 3). The daily number of snakes that emerged was adequately explained by the number of each frog species and climate

Table 1. Monthly fluctuations in the numbers of *Ovophis okinavensis* with prey in their stomachs

Month	Prey items recovered from the stomach of <i>Ovophis okinavensis</i>						
	<i>Microhyla okinavensis</i>	<i>Rhacophorus viridis</i>	<i>Polypedates leucomystax</i>	<i>Rana</i> sp.	<i>Rana narina</i>	Mammals	Lizards
Jan.	1	2	0	6	0	1	0
Feb.	0	2	0	0	0	0	0
Mar.	9	3	1	0	0	1	1
Apr.	2	0	0	0	0	0	0
May	1	0	0	0	0	0	0
June	4	0	1	0	1	0	0
July	0	0	1	0	0	0	1
Aug.	0	1	0	0	0	0	0
Sept.	0	0	0	0	0	0	0
Oct.	0	0	0	0	0	0	0
Nov.	0	0	1	1	0	0	0
Dec.	0	1	0	6	0	0	1

factors. Based on the AIC, a model including numbers of *Rha. viridis* and *M. okinavensis*, precipitation, humidity, and air temperature as explanatory terms was selected as the best-fitting

model (AIC = 168.08) (Table 2). Numbers of *Rha. viridis* and *M. okinavensis*, and humidity showed positive correlations with the number of snakes (coefficient ± S.E.: RV = 0.097 ± 0.020, MO = 0.052 ± 0.012, humidity = 0.086 ± 0.013), whereas precipitation and air temperature showed negative correlations (precipitation = -0.091 ± 0.024, air temperature = -0.087 ± 0.027).

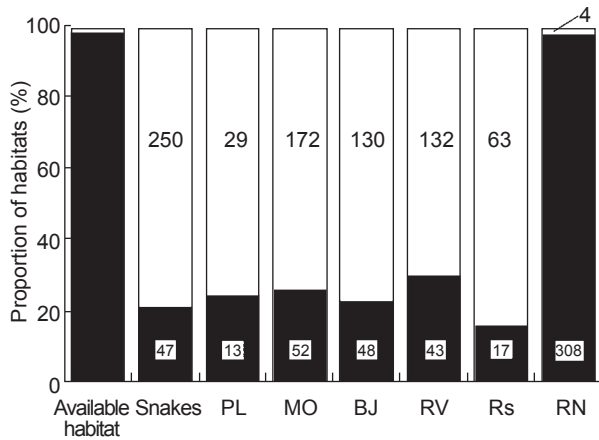


Fig. 1. Proportions of habitats available at the study site and those used by a snake (*Ovophis okinavensis*) and 6 species of frogs. PL, *Polypedates leucomystax*; MO, *Microhyla okinavensis*; BJ, *Buergeria japonica*; RV, *Rhacophorus viridis*; Rs, *Rana sp.*; RN, *Rana narina*. Black columns indicate water-gathering structure (WGS) areas, which consisted of a WGS and its surrounding area (3 m around the WGS). White columns indicate other areas, including roads, ditches, and other habitats. Numerals in columns indicate the numbers of individuals captured in each habitat (snake and frogs).

DISCUSSION

In this study, *O. okinavensis* emerged and frequently foraged in the warm season as well as in the cold season. The diet of the snakes consisted mainly of frogs (89.8%), especially *M. okinavensis*, *Rana sp.*, and *Rha. viridis*. Mori et al. (2002) showed that *O. okinavensis* at their study site predominantly exploited frogs (97.7%), mostly *Rana sp.* and *R. narina*. Thus, both the present and former studies demonstrated this snake's high dependency on frogs as a food resource. The difference in the main prey species between the 2 populations may reflect different prey availabilities between the 2 habitats.

The highly biased emergence of *O. okinavensis* and frogs, except *R. narina*, in WGS areas indicates that *O. okinavensis* and these

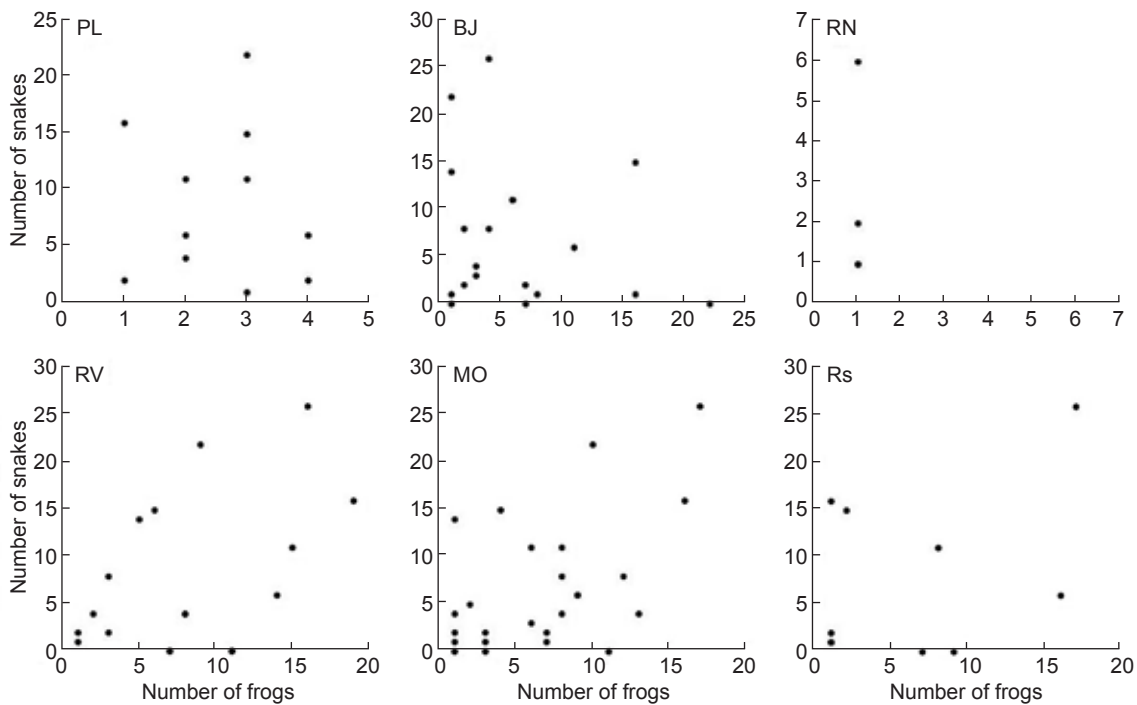


Fig. 2. Relationships between the number of *Ovophis okinavensis* and those of frogs found at each water-gathering structure (WGS). Note that in some cases, multiple WGSs are plotted at the same points. For abbreviations, see figure 1.

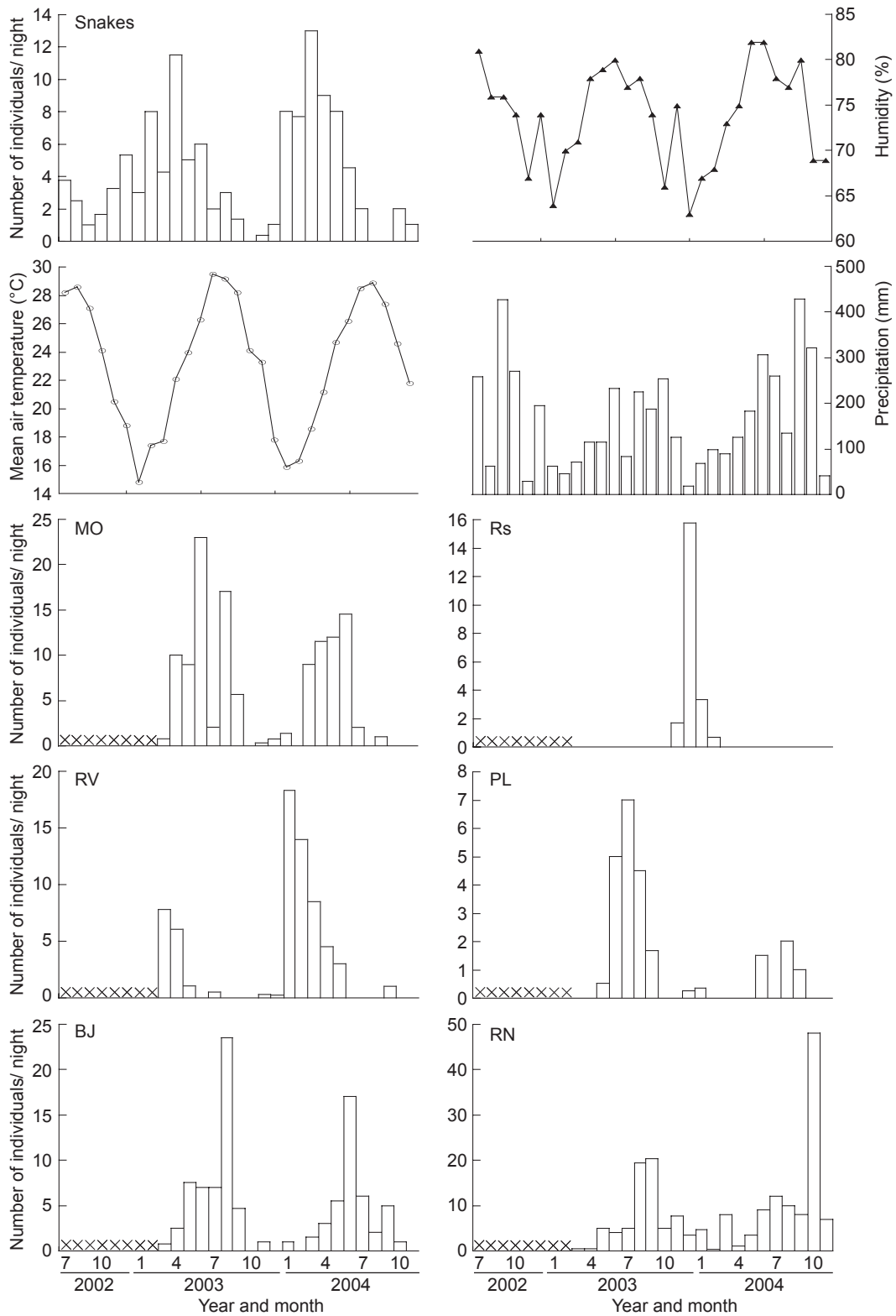


Fig. 3. Seasonal fluctuations in the numbers of *Ovophis okinavensis* and 6 species of frogs observed at the study site, and seasonal changes in meteorological features. The mean number of animals observed per night is shown for each month. The symbol, X, indicates that no frog survey was conducted in that month. Precipitation (columns), humidity (closed triangles), and air temperature (open circles) were recorded at Nago City, 40 km southwest of the study site, and were obtained from the *Weather Calendar of Okinawa, 2002-2004*, published by the Japan Weather Association, Okinawa Branch. For abbreviations, see figure 1.

frogs selectively used WGS areas. These frogs used the WGS areas for reproduction, forming dense aggregations there. In contrast, the spatial distribution of *R. narina* did not differ from random expectations based on the proportion of available areas (WGS vs. non-WGS areas). This may have been because *R. narina* did not use WGS areas as reproductive sites. Thus, the low predation frequency on *R. narina* (1 case) at this study site may simply reflect the fact that *O. okinavensis* had fewer chances to encounter *R. narina*. On the other hand, no *B. japonica* was used as prey items, although this frog highly aggregated in WGS areas. It was interesting to examine why *O. okinavensis* in the current study area did not eat such an abundant food resource in spite of the fact that *B. japonica* was reported as being the prey of *O. okinavensis* in other areas (Mishima 1966).

Positive correlations of the abundance of snakes in WGS areas with those of *Rha. viridis* and *M. okinavensis*, but not with those of other frog species, suggest that the spatial utilization (as ambushing sites) of snakes largely depended on the distributions of *Rha. viridis* and *M. okinavensis*. Furthermore, the daily emergence pattern of the snake was well synchronized with those of *Rha. viridis* and *M. okinavensis*. Thus, it was concluded that *O. okinavensis* adjusts its foraging activity to spatial and temporal fluctuations in the available frog species in a given locality regardless of season (temperature). Therefore, this suggests that the high activity of *O. okinavensis* in winter at other study sites (Ikehara and Akamine 1976, Moriguchi 1989, Mori et al. 2002) largely reflects the abundance of prey animals being restricted to the winter season rather than to a low-temperature preference, resulting in the unusual activity pattern of snakes.

Cyclophiops semicarinatus, a snake sympatric with *O. okinavensis*, shows decreased

activity in winter (Nakachi 1995). It was supposed that the abundance of the main prey (earthworms) of *C. semicarinatus* might not be markedly reduced in winter in subtropical regions because even in some temperate regions, the biomass of earthworms does not decrease in winter (Monroy et al. 2006, Millican and Lutterschmidt 2007). Thus, the low activity of *C. semicarinatus* in winter may have been due to low temperatures rather than decreased prey availability. On the other hand, Moriguchi (1989) and Mori et al. (2002) demonstrated high activities for *O. okinavensis* during the cold season and surmised that this winter activity was associated with foraging. This was also supported by my results. Furthermore, air temperatures showed negative correlations with the number of snakes, suggesting that *O. okinavensis* may prefer low temperatures for its activity. It is possible that *O. okinavensis* has some physiological tolerance (or preference) for low temperatures, at least to some extent, that enables the snake to exploit abundant food resource in the cold season in this subtropical region. The phylogenetic position of *O. okinavensis* also supports a possible physiological tolerance for low temperatures, because the most closely related species, *Trimeresurus gracilis* (Malhotra et al. 2010), lives in high-mountain areas of Taiwan (at elevations of > 2000 m; where the mean air temperature in summer is around 15°C, based on data from the Central Weather Bureau, Taiwan at <http://www.cwb.gov.tw/eng/index.htm>) (Keegan and Matsui 1964, Lin and Tu 2008). Nonetheless, it is likely that the relatively high temperatures in winter on Okinawa I. may allow correlated activity between *O. okinavensis* and its prey frogs. In any event, my results suggest that the annual activity of *O. okinavensis* largely reflects the abundance of prey animals rather than simply being affected by seasonal changes in temperature.

Table 2. Akaike information criterion (AIC) and AIC differences (Δ_i) of the best 5 alternative models explaining the daily number of snakes that emerged

Rank	Model	AIC	AIC difference (Δ_i)
1	RV, MO, rain, temperature, and humidity	168.08	0
2	RV, MO, RN, rain, temperature, and humidity	168.32	0.24
3	RV, MO, RN, PL, rain, temperature, and humidity	169.00	0.92
4	RV, MO, RN, PL, Rs, rain, temperature, and humidity	170.93	2.85
5	RV, MO, RN, PL, Rs, BJ, rain, temperature, and humidity	172.92	4.84

For species abbreviations, see the legend to figure 1.

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